

RESEARCH ARTICLE

Protecting an artificial savanna as a nature-based solution to restore carbon and biodiversity in the Democratic Republic of the Congo

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Abstract

A large share of the global forest restoration potential is situated in artificial 'unstable' mesic African savannas, which could be restored to higher carbon and biodiversity states if protected from human-induced burning. However, uncertainty on recovery rates in protected unstable savannas impedes science-informed forest restoration initiatives. Here, we quantify the forest restoration success of anthropogenic fire exclusion within an 88-ha mesic artificial savanna patch in the Kongo Central province of the Democratic Republic of the Congo (DR Congo). We found that aboveground carbon recovery after 17 years was on average $11.40 \pm 0.85 \text{ Mg C ha}^{-1}$. Using a statistical model, we found that aboveground carbon stocks take 112 ± 3 years to recover to 90% of aboveground carbon stocks in old-growth forests. Assuming that this recovery trajectory would be representative for all unstable savannas, we estimate that they could have a total carbon uptake potential of $12.13 \pm 2.25 \text{ Gt C}$ by 2100 across DR Congo, Congo and Angola. Species richness recovered to 33.17% after 17 years, and we predicted a 90% recovery at 54 ± 2 years. In contrast, we predicted that species composition would recover to 90% of old-growth forest composition only after 124 ± 3 years. We conclude that the relatively simple and cost-efficient measure of fire exclusion in

artificial savannas is an effective nature-based solution to climate change and biodiversity loss. However, more long-term and in situ monitoring efforts are needed to quantify variation in long-term carbon and diversity recovery pathways. Particular uncertainties are spatial variability in socio-economics and growing conditions as well as the effects of projected climate change.

KEYWORDS

artificial savanna, biodiversity recovery, carbon recovery, Central Africa, Congo Basin, forest restoration, nature-based solution

1 | INTRODUCTION

Central Africa is a spotlight area in the fight against climate change. On the one hand, central African forests might play an increasingly important role in mitigating climate change. They are more efficient at slowing climate change (Hubau et al., 2020), more carbon-dense (Lewis et al., 2013) and more resistant to our changing climate (Bennett et al., 2021) than other tropical forests (Jung et al., 2021). On the other hand, human pressure on central African forests might contribute to accelerating climate change. Rapidly changing climatic conditions, particularly increasing temperature and drought, lead to the loss of biodiversity (Aguirre-Gutiérrez et al., 2020) and saturation of the carbon sequestration potential (Hubau et al., 2020) of intact African rainforests. Central African forests are also facing more visible direct threats: land-use change (i.e. permanent conversion of natural ecosystems through deforestation) and land management (i.e. temporary loss through shifting agriculture, wildfire and forestry) (Curtis et al., 2018). For example, forest loss through land-use change and land management in the Democratic Republic of the Congo (DR Congo) surpasses 1 Mha per year and is expected to intensify (Mitchard, 2018; Tyukavina et al., 2018) due to the four-fold growth in local human population by the end of this century (Gerland et al., 2014; Heinrich et al., 2023).

Nature-based solutions (NBS), such as the protection of intact ecosystems in climate-resistant, moist, diverse and carbon-rich areas such as central Africa, are crucial to mitigate global warming (Girardin et al., 2021). Specifically, the restoration of forest ecosystems is gaining importance because of an increasing land area where actual carbon stocks are lower than potential carbon stocks (Lewis et al., 2019). The potential of forest restoration has been quantified by recent global studies showing that up to 205 Gt (Friedlingstein et al., 2019) of additional carbon could be stored if potentially restorable areas would be restored globally, and up to 466 Gt if other vegetation types are also considered for restoration (Erb et al., 2018). A large share of the global forest restoration potential is situated in the tropics and subtropics. Restoration of intact forests of tropical and subtropical land committed for forest restoration under the Bonn Challenge or national restoration schemes was predicted to store an additional 42 Gt of carbon by 2100 across 350 Mha. About a quarter of this additional carbon would be stored in central Africa (Lewis et al., 2019).

Despite being crucial for regulating global carbon cycling (Valentini et al., 2014) and biodiversity (Liang et al., 2022), central African forests are largely understudied in comparison to other biomes and regions (White et al., 2021). Consequently, central African carbon stocks are ill-understood, with mismatches greater than 100% between estimates (Avitabile et al., 2016; Baccini & Asner, 2014; Fisher et al., 2013; Mitchard et al., 2013; Saatchi et al., 2011). Furthermore, while carbon (Poorter et al., 2016) and biodiversity (Rozendaal et al., 2019) recovery pathways have been relatively well quantified for the Neotropics, they remain poorly understood in central Africa, barring a few pioneering studies (Bauters et al., 2019; King et al., 1997; Makelele et al., 2021). Additionally, most insights into forest restoration pathways are derived from space-for-time studies, where forest succession is quantified using different forest inventory plots at different times after abandonment (Bauters et al., 2019; Makelele et al., 2021; Poorter et al., 2016; Rozendaal et al., 2019). These so-called chronosequence studies focus on forest-rich regions, where forest losses are mostly temporary and young forests are often a result of forest regeneration directly following land disturbance (e.g. shifting cultivation) (Bauters et al., 2019; Makelele et al., 2021). As such, chronosequence studies are not necessarily representative of restoration pathways in areas that experienced permanent long-term land-use change, such as artificial savannas.

Artificial savannas are characterized by intense and regular disturbance by humans (Erb et al., 2018; Sankaran, 2019) and became widespread during the Anthropocene (Sankaran, 2019; Van Der Werf et al., 2017). Local communities rely on a multitude of goods and services provided by the savanna ecosystem, such as water, food, medicinal resources, livestock grazing, construction materials including timber and grasses and sources of energy like fuelwood and charcoal (Osborne et al., 2018; Sankaran, 2019). It has been estimated that tropical artificial savannas account for about 71% of the total global burned area and contribute to about 62% of the worldwide fire-driven carbon emissions (Van Der Werf et al., 2017; Zhou et al., 2022). As such, artificial savannas play a significant role in the yearly fluctuation of global atmospheric CO₂ levels (Zhou et al., 2022). Therefore, reducing fire regimes in artificial savannas is often seen as a promising strategy for increasing forest carbon sequestration, and these ecosystems are being considered in restoration initiatives aimed at climate change mitigation (Bastin et al., 2019; Zhou et al., 2022). The success of restoration

in artificial savannas is determined by many factors, including water availability and the extant regime of (fire) disturbance (Erb et al., 2018; Sankaran et al., 2005).

Artificial savannas contribute about a quarter of the mismatch between potential and actual global biomass stocks (Erb et al., 2018). Savannas are 'unstable' systems if mean annual precipitation (MAP) exceeds 650 mm, which is sufficient for woody canopy closure (Sankaran et al., 2005; Staver et al., 2011). They are therefore also referred to as 'mesic' (seasonally wet) savannas. Discontinuing artificial burning regimes may allow forests to recolonize savannas, which has been shown through fire exclusion experiments in the Kruger National Park in South Africa (Higgins et al., 2007; Zhou et al., 2022), in the Cerrado savannas in Brazil (Abreu et al., 2017; Moreira, 2000; Silva et al., 2013) and within the Calabozo Reserve in Venezuela (San Jose et al., 1998; San Jose & Farinas, 1983). However, apart from a single study in Gabon (King et al., 1997), no fire exclusion experiments have been documented in the mesic savannas of central Africa, impeding the evaluation of the forest recovery potential of a vast area of land in that region. Therefore, scientists and policy-makers lack important knowledge for the implementation of forest restoration (Makelele et al., 2021). Detailed long-term experimental plots in regrowing forests will contribute to designing successful restoration strategies in the Congo Basin to mitigate climate change (Aide et al., 2000; Rozendaal & Chazdon, 2015).

Here, we quantified the forest restoration success of a fire exclusion experiment within an artificial mesic savanna in the Kongo Central province of DR Congo (MAP of 1180 mm year⁻¹). The experiment was set up in 2005, when the annual burning regime in an 88-ha savanna patch was discontinued (Deklerck et al., 2019). We installed 101 permanent inventory plots, which were measured in 2010, 2014 and 2022, covering 17 years of forest restoration. Additionally, we used the data from three savanna plots near the experiment and 19 old-growth plots from the nearby UNESCO MAB reserve of Luki as a reference. These reference plots are assumed to be representative of the start and endpoint of forest regeneration in the fire exclusion experiment (Deklerck et al., 2019). This study aimed to (i) evaluate the success and rate of forest carbon stocks recovery; (ii) quantify the recovery of tree species richness and species composition; and (iii) predict the long-term recovery trajectories of forest carbon stocks, species richness and composition in artificial (mesic) African savannas under fire protection. Finally, we aimed to (iv) use the carbon recovery trajectory to estimate the total carbon sequestration potential of fire exclusion in artificial, unstable savannas across DR Congo, Congo and Angola.

2 | METHODS

2.1 | Permanent inventory plots in the Manzonzi fire exclusion

To limit the expansion of savanna fires and contribute locally to the restoration of degraded forest ecosystems in the periphery of the Luki reserve, the local community of Manzonzi village established a

contiguous 88-ha fire exclusion area within the 200 ha of the Manzonzi artificial savanna patch in 2005 with the support of WWF-DR Congo (Deklerck et al., 2019) (Figure S1). The entire boundary of this fire exclusion area is periodically cleared manually by the local community members to avoid bushfires and grazing (Deklerck et al., 2019). To increase our understanding of carbon and biodiversity dynamics in this savanna ecosystem, a systematic sampling plot design was set up in 2010 and arranged into 10 parallel north-south transects spread over the contiguous 88-ha fire exclusion. Along the transects, a total of 101 permanent inventory plots were installed, measuring 50 m by 80 m each, with 20 m between the plots (Figure S1). The total monitored area in 2010 was 40.4 ha, with each plot being 0.4 ha (Deklerck et al., 2019). However, between 2010 and 2022, 14 plots were transformed back into agricultural land to meet some needs of the local community. Therefore, only the 87 undisturbed plots (comprising 34.8 ha) are considered in this study. We refer to Data S1 for a more detailed description of the vegetation and climate of the study region.

In each plot, all live stems with a diameter greater than 100 mm were tagged, measured for diameter at breast height at 1.3 m or above buttresses and identified up to species level using standard forest inventory protocols (ForestPlots.net et al., 2021). Species identification was carried out with the help of local botanists of the *Institut National pour l'Etude et la Recherche Agronomiques* (INERA), based in the Luki-INERA station. The inventories of 2022 followed the same protocol as those of 2010 and 2014. Trees that grew larger than the diameter of 100 mm during a period between censuses were recorded as recruits, tagged and their DBH was measured.

2.2 | Reference plots

Three 'savanna reference plots' of equal dimensions (0.4 ha; 50 m by 80 m) were established outside the fire exclusion, using the same inventory protocol. These savanna plots are not protected against burning or grazing, and the savanna vegetation is maintained. Therefore, these plots serve as a reference for the starting point of forest regeneration (0 years after fire exclusion). In addition, 19 'old-growth forest reference plots' (hereafter 'OGF plots') were installed in the central zone of the Luki reserve following the same method, although these plots are larger (1 ha; 100 by 100 m). The Luki OGF plots can be considered as old growth because radiocarbon dates on charcoal found in the top soil of pits excavated near some of the plots yielded ages of 525 calendar years before present or older (Hubau et al., 2013, 2015). We assumed that the Luki OGF plots could be considered as a reference for the endpoint of forest succession.

2.3 | Tree species classification

Tree species names were verified in accordance with the African Plants Database (Hubau et al., 2020; Lewis et al., 2009). We grouped all tree species in the plot data into two main categories, namely 'savanna specialist' and 'forest specialist' species,

based on literature sources reporting on species-specific ecology of the Mayombe forests (Donis, 1948; Lubini, 1997), the Bas-Congo (Compère, 1970), the Lower Guinea (Hawthorne, 1995; Meunier et al., 2015) and central Africa (Doucet, 2003; Lebrun & Gilbert, 1954; Toussaint et al., 1953) (Table S1). Additional information was collected from online databases (African Plant Database, 2023, <https://africanplantdatabase.ch/>). Savanna specialist species typically occur in open and dry woodland formations or tree savanna. Forest specialist species are representative of all stages of forest succession. They are further classified according to their guild: short-lived pioneers, long-lived pioneers, non-pioneer light demanders, shade-tolerant species (Deklerck et al., 2019) and according to their seed dispersal mechanism (Table S1).

2.4 | Forest structural metrics

Our analysis was done in R version 4.1.2 (R Core Team, 2018). The aboveground biomass (AGB, in Mg stem⁻¹) of each tree was estimated with an allometric equation for moist tropical forest (Chave et al., 2014): $AGB = \left(0.0673 \times (\rho \times DBH^2 \times H_t)^{0.976} \right) / 1000$, where ρ is wood density (g cm⁻³), DBH is tree diameter at breast height (cm) and H_t is the total tree height (m). Wood density values were derived from the Global Wood Density Database on the Dryad digital repository (Chave et al., 2009; Zanne et al., 2009). For incompletely identified trees (0.04%) or for trees belonging to species not in the wood density database (41.23%), we used the mean density value for the next-highest known taxonomic category (genus or family, as appropriate). For unidentified trees (0.02%), we used the mean wood density value of all individual trees in the plots (Hubau et al., 2020; Lewis et al., 2009). A central African height-diameter allometry was used to calculate the total individual tree height (H_t , in m) (Feldpausch et al., 2011): $H_t = 50.4531 \times \left(1 - \exp \left(-0.0471 \times DBH^{0.81197} \right) \right)$. Aboveground biomass values were then converted to aboveground biomass carbon stocks (AGC, in Mg C ha⁻¹) using the mean carbon fraction for tropical angiosperms (i.e. 45.6%) (Martin et al., 2018). Plot-level AGC was then obtained by summing AGC across all trees within each plot, divided by the plot area (ha). Plot-level absolute aboveground carbon stocks (AGC) of forest specialist species (green) and savanna specialist species (orange) are visualized using violin distributions (Figure 1a,b). For each Manzonzi census, we calculated the mean plot-level values and standard error of AGC (Mg C ha⁻¹), stem density (N, tree⁻¹), DBH (mm, tree⁻¹) and basal area (m² ha⁻¹) by using the R package *dplyr* (Mailund, 2019). These variables were determined for each species category (forest and savanna specialists), and the results are shown in Table 1. We calculated the same metrics for the savanna and old-growth reference plots (Table 2).

For each Manzonzi census, plot-level relative aboveground carbon stocks were then calculated as the absolute AGC divided by the median AGC of the 19 old-growth forest reference plots in the Luki reserve, multiplied by 100 (Figure 1c,d).

2.5 | Tree diversity metrics

Species richness and species composition are important indicators for assessing the speed of biodiversity recovery (Rozendaal et al., 2019). We calculated both absolute and relative species richness and species composition for each census (5, 9 and 17 years after fire exclusion) for each of the 87 non-disturbed plots. Absolute plot-level species richness (Figure S2) was calculated using the R package *vegan* (Marcon, 2015). We also calculated the species richness of the Luki OGF plots and the savanna reference plots. Due to the difference in plot area (0.4 ha for the Manzonzi plots and 1 ha for the Luki OGF plots), we calculated the rarefied species richness of the Luki OGF plots to express species richness at 0.4 ha (Poorter et al., 2021; Rozendaal et al., 2019). Relative plot-level species richness (Figure 2a,b) in the Manzonzi plots and control plots is then defined as the absolute plot-level species richness divided by the median of species richness of the Luki OGF plots multiplied by 100 (Rozendaal et al., 2019).

Relative plot-level species composition (Figure 2c,d) in the Manzonzi experiment was calculated as the mean pairwise similarity in species composition between each plot ($n=87$) and the 19 Luki OGF plots, divided by the median number of species composition of the Luki OGF plots, multiplied by 100 (Rozendaal et al., 2019).

In addition to species richness and species composition, we calculated multiple commonly used diversity indices to assess the shift of species diversity in the Manzonzi experiment compared to the reference values of the savanna reference plots and the Luki OGF plots: Pielou's evenness, Shannon-Weaver index, Simpson index and Fisher Alpha diversity index (Kearsley, 2015; Morris et al., 2014; Shannon, 1948; Simpson, 1949; Sullivan et al., 2020) (Tables 1 and 2).

2.6 | Statistical analysis

We applied a non-parametric Kruskal-Wallis test to compare the mean of each forest structural and biodiversity metric across censuses. We applied Tukey's HSD (honestly significant difference) test to account for multiple comparisons of means (Ostertagová et al., 2014) (Figures 1a,b and 2a,c; Figure S2).

We parameterized long-term forest recovery trajectories of carbon and biodiversity metrics using the savanna reference plots ($t=0$ year) and the 2010 ($t=5$), 2014 ($t=9$) and 2022 ($t=17$) plot-level estimates from the Manzonzi plots with the plot-level estimates of the Luki OGF plots ($t=525$) as a reference. We parameterized the recovery trajectories of structural and biodiversity metrics as a function of forest age (years after fire exclusion) using the Gompertz model: $A_t = A_{start} + ((A_{OGF} - A_{start}) \times \exp(-1 \times \exp(-k \times (t - \text{infl}))))$, where A_t is the metric value at a given time after fire exclusion (t , in year), A_{start} is the metric value at the start of the monitoring period (In this study, A_{start} corresponds to the plot-level average AGC of our three savanna reference plots), A_{OGF} is the asymptotic 'old-growth forest' maximum value of the metric and k represents the slope of the recovery curve at the point of

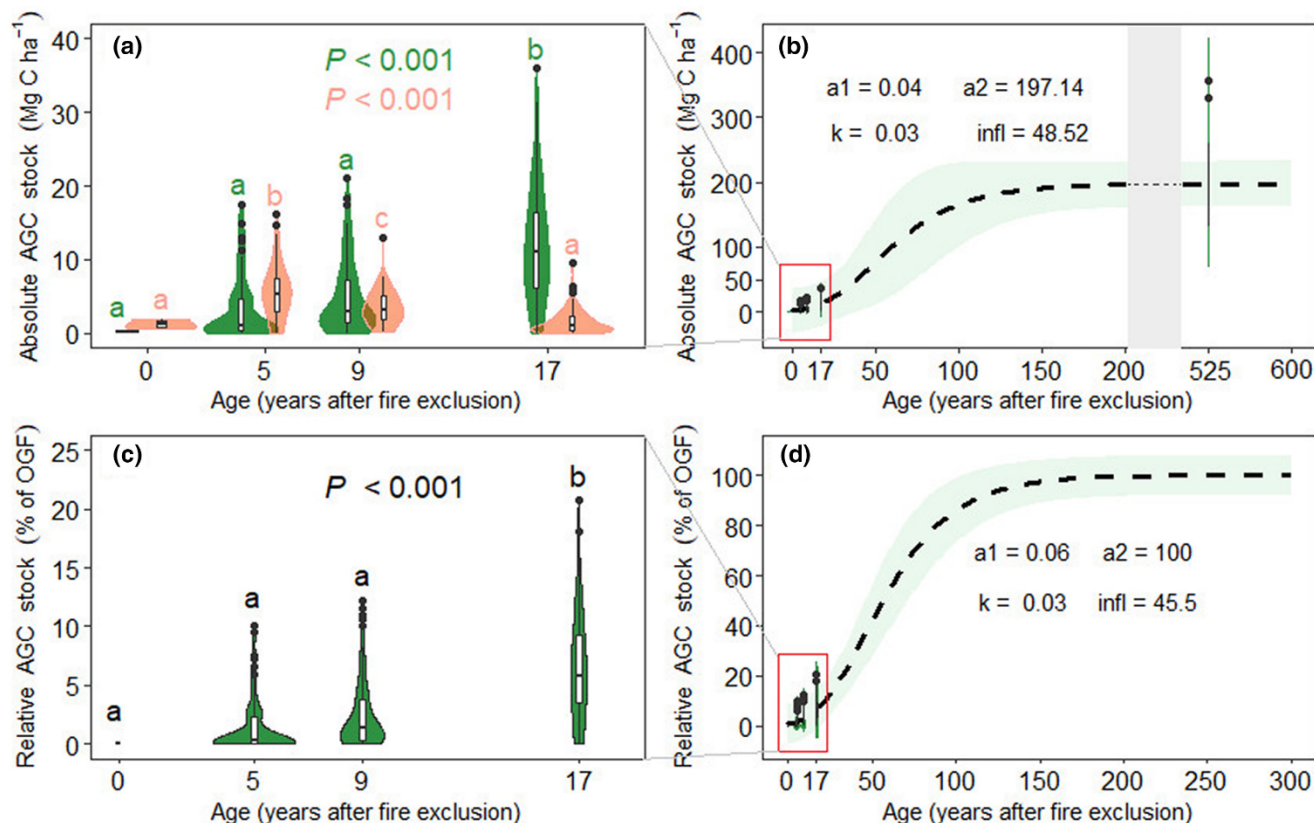


FIGURE 1 Aboveground carbon recovery. (a) Violin distribution of plot-level absolute aboveground carbon stocks (AGC) of forest specialist species (green) and savanna specialist species (orange) after 0, 5, 9 and 17 years of fire exclusion in the Manzonzi experiment, corresponding to the savanna plots and the 2010, 2014 and 2022 censuses, respectively. Violin shapes show the distribution of AGC stocks across the plots; white boxplots show the median and the 25th and 75th percentiles. The p -value is from a Kruskal-Wallis test; letters above violin plots indicate if there is a significant difference ($p < .05$) between AGC stocks across the monitoring years, according to Tukey's test. (b) Prediction of the long-term recovery trajectory of absolute aboveground carbon stocks (AGC) of forest specialist species using the Gompertz model. Shading corresponds to the 95% confidence interval (CI). (c) Violin distribution of plot-level relative aboveground carbon stocks (AGC) of forest specialist species, defined as the absolute AGC divided by the median AGC of the 19 old-growth forest (OGF) plots in the Luki reserve, multiplied by 100. (d) Prediction of the long-term recovery trajectory of relative aboveground carbon stocks (AGC).

inflection (infl) (Deklerck et al., 2019). Model parameterization was performed using the R package *Stats* (Deklerck et al., 2019; R Core Team, 2018). A sensitivity analysis testing the effect of uncertainties in the age of the Luki OGF plots is presented in Data S1 and Figure S3. Furthermore, we also predicted the absolute AGC using a logarithmic instead of a Gompertz model (Poorter et al., 2016; Rozendaal et al., 2019) (Data S1; Figure S4).

Lastly, using a simple linear regression model and Kendall's tau correlation test, we investigated the bivariate relationship between absolute aboveground carbon stocks and absolute species richness using the Manzonzi and Luki datasets and the bivariate relationship between relative species richness (% of OGF) and relative species composition (% of OGF) (Sullivan et al., 2017) (Figure 4). Kendall's tau correlation is a non-parametric test, meaning that it does not assume bivariate normality and can handle ties (Sullivan et al., 2017). It ranges from -1 to 1 , where -1 indicates a perfect negative correlation, 0 indicates no correlation and 1 indicates a perfect positive correlation (Taylor, 1987).

2.7 | Upscaling analysis

The Manzonzi enclosure experiment presented here provides the first ground-based data describing carbon recovery after the protection of artificial mesic savannas in central Africa. We used the predicted trajectory in Figure 1b to roughly predict the total potential carbon uptake of similar savannas if they would be protected from further disturbance (grazing and burning). We focused on the countries containing (DR Congo) and immediately surrounding (Angola and the Republic of the Congo) our research area. For this upscaling analysis, we combined three spatial products: a vegetation map, a precipitation map and a biomass map.

First, we used the Global Land Cover Map 2009 (GLOBCOVER) (Harper et al., 2023) and White's vegetation map of Africa (White, 1983) to extract pixels classified as savanna (see Table S2 for an overview of land cover types classified as savanna in each of the products). To match with the gridded products described below, GLOBCOVER was down-sampled from 300m to 30 arcsec (~ 1 km).

TABLE 1 Plot-level structural and biodiversity metrics of the 87 permanent plots of the Manzonzi regeneration experiment. Mean values of aboveground carbon (AGC), stem density (N), diameter at breast height (DBH), basal area (BA) and biodiversity metrics are quantified at the plot level and for each species category. The uncertainty indicates the standard error. The different letters indicate the post-hoc (Tukey's HSD) statistical significant differences ($p < .05$); the absence of common letters indicates a significant difference between the considered static metrics.

Variable	Species category	2010	2014	2022
AGC (MgCha ⁻¹)	Savanna specialist	5.50±0.39 ^a	3.25±0.26 ^b	1.43±0.18 ^c
	Forest specialist	2.89±0.67 ^a	4.67±0.71 ^a	11.40±0.85 ^b
	All categories	8.39±0.40 ^a	7.92±0.38 ^a	12.83±0.58 ^b
N (treesha ⁻¹)	Savanna specialist	119.51±9.05 ^a	53.16±3.91 ^b	23.73±3.39 ^c
	Forest specialist	34.22±6.04 ^a	66.90±6.72 ^b	170.00±10.46 ^c
	All categories	153.73±6.32 ^a	122.88±3.91	193.73±7.81 ^c
DBH (mm tree ⁻¹)	Savanna specialist	129.62±2.58 ^a	130.18±4.54 ^a	128.17±3.96 ^a
	Forest specialist	115.54±7.99 ^a	127.41±6.25 ^{ab}	144.16±6.16 ^b
	All categories	122.58±4.22 ^a	128.80±3.85 ^{ab}	136.16±3.70 ^b
BA (m ² ha ⁻¹)	Savanna specialist	24.34±0.02 ^a	12.42±0.02 ^b	5.33±0.02 ^c
	Forest specialist	11.78±0.03 ^a	20.05±0.02 ^b	49.81±0.01 ^b
	All categories	18.06±0.02 ^a	16.24±0.02 ^a	27.57±0.03 ^b
Simpson's index	All categories	0.64±0.02	0.80±0.02	0.83±0.01
Shannon index	All categories	1.36±0.06	2.00±0.08	2.35±0.47
Pielou's evenness	All categories	0.71±0.13	0.81±0.11	0.72±0.05
Species richness	All categories	7.54±0.39	17.29±1.38	27.66±0.91
Fisher's α	All categories	2.55±1.56	3.99±2.00	7.26±2.98

In a second step, we extracted mean annual precipitation (MAP) for each savanna pixel from WorldClim version 2.1 (Library et al., 2017) to categorize the savanna into one of three types: stable (arid) savannas (MAP <516mm/year), the transition between stable and unstable savannas (516mm/year < MAP < 783mm/year) and unstable (mesic) savannas (MAP > 783mm/year) (Sankaran et al., 2005). We focused further analysis on unstable savanna pixels only, as these are assumed to potentially store additional carbon if protected from disturbance and are assumed to have similar environmental conditions. We then used the Gompertz model from the fire exclusion experiment of Manzonzi (Figure 1b) to quantify the total potential carbon storage from natural forest regeneration by 2100 in the hypothetical event that all unstable savanna pixels in these three countries would be protected starting in 2025. This corresponds to a total recovery period of 75 years and a total potential carbon stock of 130.34MgCha⁻¹ for each unstable savanna pixel (Figure 1b).

In a third step, we extracted the actual (present-day) aboveground biomass for each unstable savanna pixel from an aboveground carbon density map for the year 2010 (Spawn et al., 2020). We first reduced the resolution from 300m to 30arcsec (~1km). For each pixel, we then subtracted the actual aboveground carbon stock from the total potential aboveground carbon stock to finally calculate the potential additional aboveground carbon storage by 2100, in MgCha⁻¹ (Figure 5). Pixels with negative values for the potential additional aboveground carbon storage were excluded from the analysis.

For each country, we then calculated the mean potential additional carbon storage (in MgCha⁻¹) using all unstable savanna pixels and multiplied it by the total unstable savanna surface area (in ha) to calculate the total country-level potential additional carbon stock in Gt C (Table 3). The standard error was calculated based on error propagation using the uncertainty values of the aboveground carbon density and the 95% confidence interval of the Gompertz model, which was converted to the standard error by dividing by 3.92 (Figure S5). To explore sensitivity owing to the selection of the climatology product, we repeated the analysis based on MAP data from 'Climatologies at High resolution for the Earth's Land Surface Areas' (CHELSA) (Karger et al., 2017) (Table S3).

3 | RESULTS

3.1 | Recovery of carbon stock

Savanna reference plots have low amounts of total carbon stored in trees, at 1.28±0.37MgCha⁻¹, as compared to 8.39±0.40MgCha⁻¹ in the first census of the Manzonzi regenerating forest plots (Tables 1 and 2; Figure 1a). Total carbon stored in trees in the Manzonzi forest regeneration experiment did not change ($p = .929$) over the first 4 years of monitoring, from 8.39±0.40MgCha⁻¹ in 2010 to 7.92±0.38MgCha⁻¹ in 2014 (Deklerck et al., 2019), but increased significantly ($p < .001$) over the next 8 years to 12.83±0.58MgCha⁻¹ in 2022 (Table 1; Figure 1a). The significance of time on the rate of

TABLE 2 Plot-level structural and biodiversity metrics of the three savanna reference plots and the 19 reference plots within the Luki old-growth (OGF) forest.

Variable	Reference plot type	Species category	Value
AGC (MgCha ⁻¹)	Savanna reference	Savanna specialist	1.24 ± 0.4
	Savanna reference	Forest specialist	0.04
	Savanna reference	All categories	1.28 ± 0.37
	Luki OGF forest	All categories	187.14 ± 68.25
N (trees ha ⁻¹)	Savanna reference	Savanna specialist	35.83 ± 8.21
	Savanna reference	Forest specialist	0.83
	Savanna reference	All categories	27.5 ± 10.2
	Luki OGF forest	All categories	490.0 ± 79.58
DBH (mm tree ⁻¹)	Savanna reference	Savanna specialist	117.08 ± 4.94
	Savanna reference	Forest specialist	144.9
	Savanna reference	All categories	124 ± 7.78
	Luki OGF forest	All categories	232.2 ± 29.69
BA (m ² ha ⁻¹)	Savanna reference	Savanna specialist	1.23 ± 0.12
	Savanna reference	Forest specialist	0.04
	Savanna reference	All categories	1.27 ± 0.13
	Luki OGF forest	All categories	31.32 ± 6.95
Simpson's index	Savanna reference	All categories	0.51 ± 0.06
Shannon index	Savanna reference	All categories	0.77 ± 0.10
Pielou's evenness	Savanna reference	All categories	0.82 ± 0.10
Species richness	Savanna reference	All categories	2.67 ± 0.33
Fisher's α	Savanna reference	All categories	1.74 ± 0.0
Simpson's index	Luki OGF forest	All categories	0.93 ± 0.01
Shannon index	Luki OGF forest	All categories	3.38 ± 0.08
Pielou's evenness	Luki OGF forest	All categories	0.80 ± 0.01
Species richness	Luki OGF forest	All categories	67.84 ± 2.82
Fisher's α	Luki OGF forest	All categories	21.82 ± 1.30

carbon sequestration is even more visible when comparing savanna specialist species with forest specialist species. Savanna specialist have been dying rapidly since the start of the experiment, decreasing from $119.51 \pm 9.05 \text{ trees ha}^{-1}$ in 2010 to only $23.73 \pm 3.39 \text{ trees ha}^{-1}$ in 2022 (Table 1). This resulted in significant ($p < .001$) carbon losses of $5.50 \pm 0.39 \text{ MgCha}^{-1}$ in 2010 to $1.33 \pm 0.18 \text{ MgCha}^{-1}$ in 2022 (Table 1; Figure 1a). In contrast, stem counts of forest specialist increased from $0.84 \text{ trees ha}^{-1}$ in the savanna reference plots to $34.22 \pm 6.04 \text{ trees ha}^{-1}$ in 2010 to $170.00 \pm 10.46 \text{ trees ha}^{-1}$ in 2022 (Tables 1 and 2). This resulted in forest specialist carbon uptake from $2.89 \pm 0.67 \text{ MgCha}^{-1}$ in 2010, to $4.67 \pm 0.71 \text{ MgCha}^{-1}$ in 2014 and then to $11.40 \pm 0.85 \text{ MgCha}^{-1}$ in 2022 (Table 1; Figure 1a). Mean diameter at breast height (DBH) showed a rather slow increase in the forest specialist class, from $115.54 \pm 7.99 \text{ mm}$ in 2010 to $144.16 \pm 6.16 \text{ mm}$ in 2022 (Table 1). The mean DBH in the savanna specialist class did not change. Basal area (BA) significantly increased for forest specialist ($p < .001$) and decreased for savanna specialist ($p < .001$; Table 1).

Using forest carbon stocks data from 19 old-growth forest (OGF) plots of the Luki reserve as a reference for the end of succession, we estimated that 0.73%, 1.61%, 2.75% and 6.57% of OGF aboveground carbon stocks were present in Manzonzi after

0, 5, 9 and 17 years of savanna protection, respectively (Tables 1 and 2; Figure 1c). We predict that aboveground carbon stocks need 56 ± 2 years to recover 50% of old-growth values (point of inflection 'infl' in Figure 1d) and 112 ± 3 years to recover 90% of old-growth values (Figure 1d).

3.2 | Recovery of species richness and composition

The average absolute species richness at the plot level increased from 0.33 in savanna reference plots, to 4.29 ± 0.49 in 2010 and then to 15.43 ± 0.64 in 2022. (Figure S2). Relative species richness increased significantly after 17 years ($p < .001$), from 0.71% of OGF species richness in the savanna reference plots, to 9.14% 2010 to 32.87% in 2022 (Figure 2a).

There are also remarkable changes in species composition. Savanna specialist represent 97.73% of the total stem density in the savanna reference plots, but they decreased quickly during forest regeneration (Figure 3a). Most notably, *Maprounea africana* Müll. Arg., which was the most abundant savanna specialist in the savanna control plots (31.82% of the total number of stems) and in the first census (2010) of the Manzonzi regeneration experiment (38%),

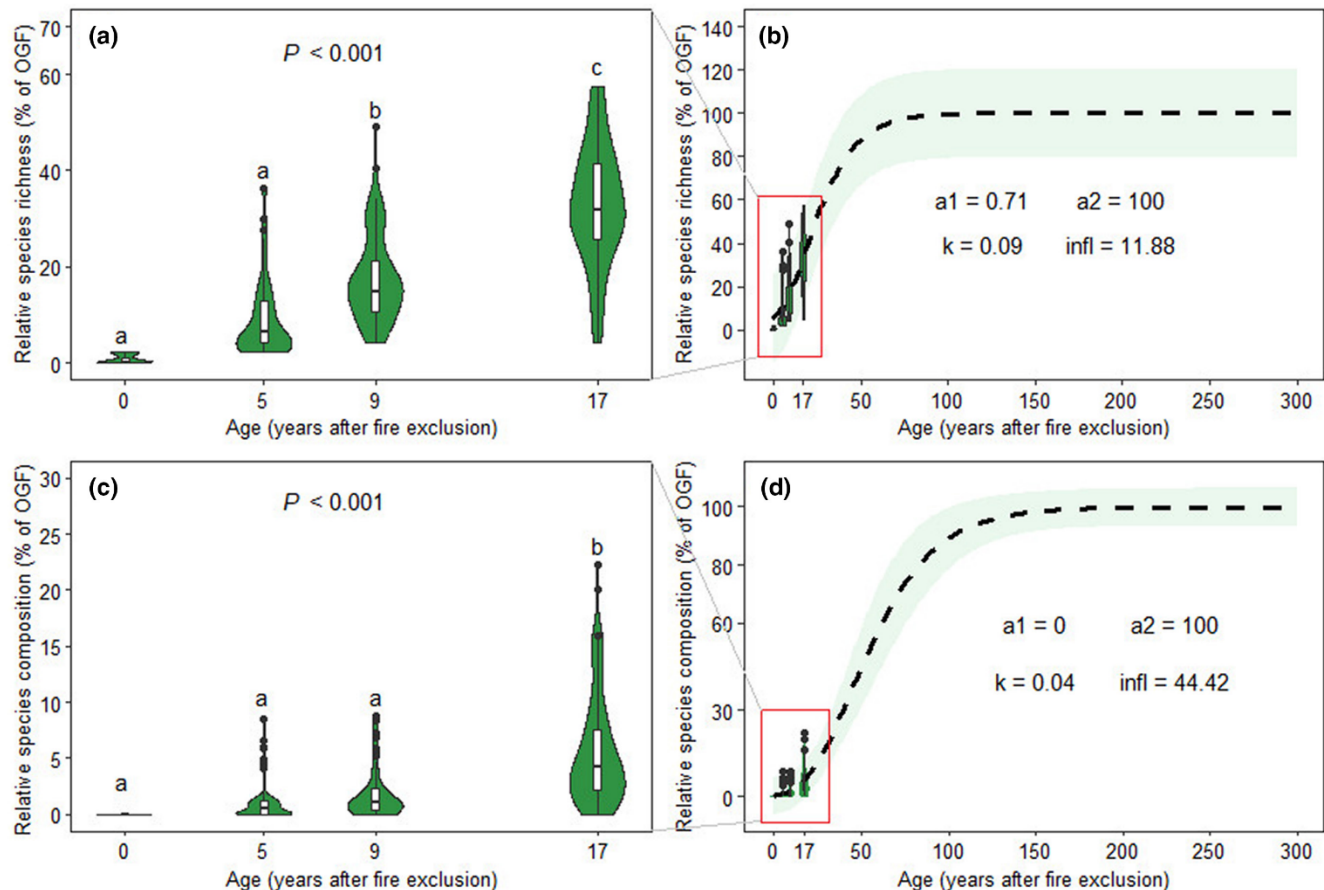


FIGURE 2 Tree species diversity recovery. (a) Violin distribution of plot-level relative species richness of forest specialist species after 0, 5, 9 and 17 years of fire exclusion in the Manzonzi experiment. Relative plot-level species richness is defined as the absolute species richness divided by the median of rarefied absolute species richness of 19 old-growth forest (OGF) plots from Luki, multiplied by 100. Violin shapes represent the distribution of species richness across the plots; white boxplots include the median and the 25th and 75th percentiles. The p -value is from a Kruskal–Wallis test; letters indicate a significant difference ($p < .05$) between monitoring years, according to Tukey's HSD test. (b) Prediction of the long-term recovery trajectory of relative species richness. Shading corresponds to the 95% confidence interval (c). (c) Violin distribution of plot-level relative species composition (expressed as % of old-growth forest) of forest specialist species. (d) Prediction of the long-term recovery trajectory of relative species composition using the Gompertz model.

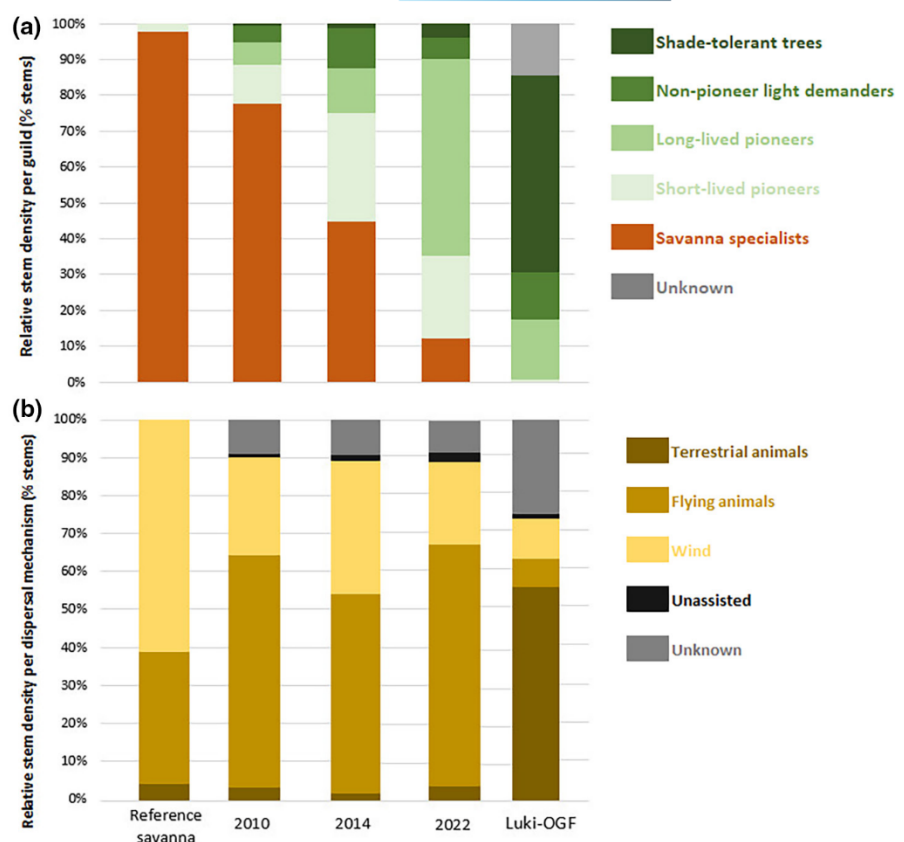
showed a net decrease from 58.2 to 1.4 stems ha^{-1} between 2010 and 2022 (Table S1). The stem density of forest specialist short-lived pioneer trees first increased from 10.71% in 2010 to 29.94% in 2014, then decreased again to 22.89% in 2022 (Figure 3a). In contrast, the stem density of long-lived pioneer trees increased significantly, from 6.21% in 2010 to 12.25% in 2014 and then to 54.38% in 2022.

However, the species composition of old-growth forest recovers remarkably slowly. Between 2010 and 2022, a total of 35 new forest specialist species appeared in the experiment (Table S1). From those, only 24 occur in the reference old-growth plots of the Luki reserve (Table S1). Shade-tolerant trees (typical for old-growth forest) increase very slowly, from almost 0% in the savanna reference plots, to 0.64% in 2010, to 1.32% in 2014 and then to 4.00% in 2022 (Figure 3a). To compare, the old-growth plots in the Luki forest are dominated by shade-tolerant trees, at 55.02% of the stems (Figure 3a). As such, after

17 years of forest regeneration, only 5.51% of the species composition of the old-growth forest of the Luki reserve recovered (Figure 2a; Table 1). The slow recovery of species composition is also apparent when looking at the dispersal mechanisms, which shows very little increase in species dispersed by large animals (Figure 3b).

After 17 years, the fire exclusion experiment of Manzonzi recovered 33.17% of the species richness of the old-growth forest of the Luki reserve (Figure 2a), while only 5.55% of the species composition was recovered (Figure 2c). We predict that species richness recovers to 50% after 25 ± 2 years (Figure 2b), while species composition recovers to 50% only after 64 ± 2 years (Figure 2d). We predict that 90% of the species richness of the old-growth forest of the Luki reserve will be recovered after 54 ± 2 years (Figure 2b). However, we predict that 124 ± 3 years will be required to recover 90% of the species composition of old-growth forest (Figure 2d).

FIGURE 3 Evolution of functional composition in the fire exclusion experiment of Manzonzi, compared to functional composition in the savanna reference plots (left) and the Luki old-growth forest (right). See Table S1 for data by species.



3.3 | Carbon–biodiversity relationships

In the fire exclusion experiment of Manzonzi, the relationship between absolute AGC stocks and species richness is positive ($R^2 = .59$, $p < .001$; Figure 4a,b) as well as between relative species composition and relative species richness ($R^2 = 0.67$, $p < .001$; Figure 4c). In contrast, no such relationship is observed between absolute AGC stocks and species richness in the reference old-growth forest plots of the Luki reserve ($R^2 = .001$, $p = .879$; Figure 4a). Additionally, Kendall's tau statistic showed a significant positive correlation ($p < .001$) between absolute AGC and species richness for each census period in Manzonzi (inset table in Figure 4a).

3.4 | Upscaling analysis

We found a total amount of actual (present-day) AGC of 3.45 ± 1.58 Gt C across 119.2 Mha of unstable artificial savanna in DR Congo, Congo and Angola (Figure 5; Table 3). In these savanna regions, the overall potential additional aboveground carbon uptake by 2100 is estimated at 12.13 ± 2.25 Gt C (Figure 5; Table 3). The highest aboveground carbon storage potential was in unstable savannas in Angola across 56.36 Mha, while the lowest values were in Congolese savannas covering only 7.22 Mha (Table 3). Sensitivity

analysis using another climatology product (i.e. CHELSA) resulted in smaller unstable savanna area in the three countries and a slightly lower potential additional aboveground carbon uptake by 2100, at 9.95 ± 2 (Table S3).

4 | DISCUSSION

4.1 | Rapid carbon recovery

Carbon accumulation in Manzonzi does not show a linear but rather an exponential pathway during the monitoring period (Figure 1), which is in line with other studies analysing long-term carbon recovery in secondary forests (Makelele et al., 2021; Poorter et al., 2016). The third census of the plots shows that predicted long-term carbon accumulation is not as fast (56 ± 2 years to recover 50% of old-growth values; Figure 1) as the pathways calculated using the first two censuses only (37 years to recover 50% of old-growth values) (Deklerck et al., 2019), showing that longer-term monitoring leads to different and probably more accurate predictions.

Carbon recovery in Manzonzi is slow as compared to rates in Neotropical chronosequences, where a median time of 66 years is needed to recover 90% of old-growth forest (Poorter et al., 2016), as compared to an estimated 112 ± 3 years in Manzonzi. This discrepancy

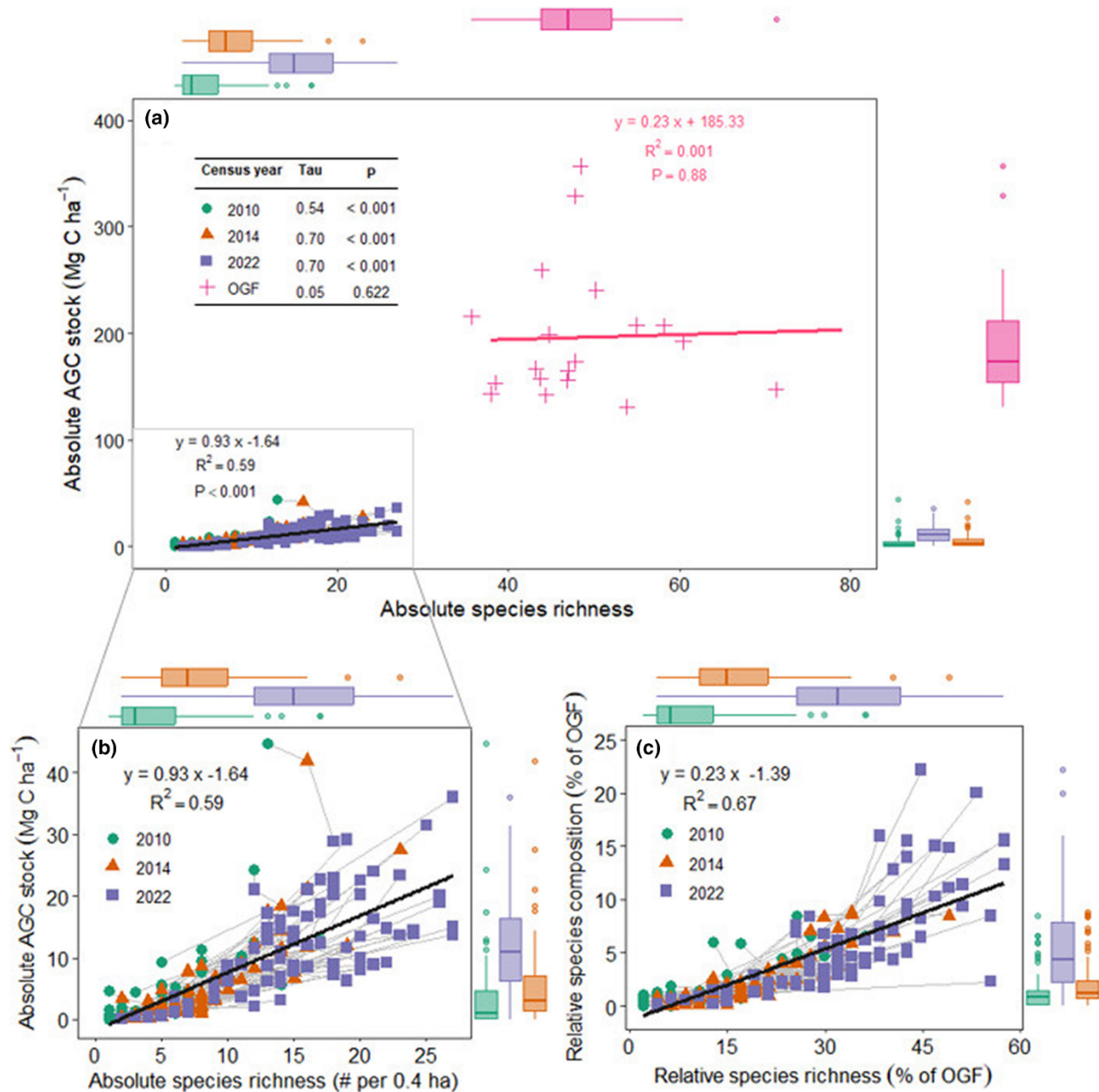


FIGURE 4 The relationship between absolute aboveground carbon stocks and absolute species richness (a and b) and between relative species composition and relative species richness (c). Different symbols refer to different datasets: green circles=Manzonzi savanna plots in 2010 ($n=87$), orange squares=Manzonzi savanna plots in 2014 ($n=87$), purple triangles=Manzonzi savanna plots in 2022 ($n=87$) and pink crosses=Luki old-growth plots ($n=19$). A thin grey line connects the three censuses for each plot. The solid black lines show a simple linear regression model on the Manzonzi data. The solid pink line (a) shows a simple linear regression model on the Luki data. The inset table in (a) reports Kendall's tau correlations between aboveground carbon stocks and species richness in the Manzonzi experiment (Sullivan et al., 2017).

could be attributed to the difference in land history. Chronosequences mostly document forest recovery after recent change (e.g. shifting agriculture), with the benefit of directly available resources (e.g. soil seed bank, tree stumps, roots from which trees establish, remnant trees that attract seed dispersal agents) (King et al., 1997; Rozendaal et al., 2019). In contrast, our experiment documents the recovery of forest in an area that had been converted to a savanna a long time ago

and where a typical savanna vegetation was established. This savanna vegetation consisted of savanna specialist trees but also tall grasses, which could possibly slow down the recruitment of forest specialist trees. Savanna specialist tree species disappear quickly in Manzonzi, but they have been present for at least 20 years (Figure 1).

Yet carbon recovery in Manzonzi is faster than in a 60-year fire exclusion experiment in the Kruger National Park (South Africa),

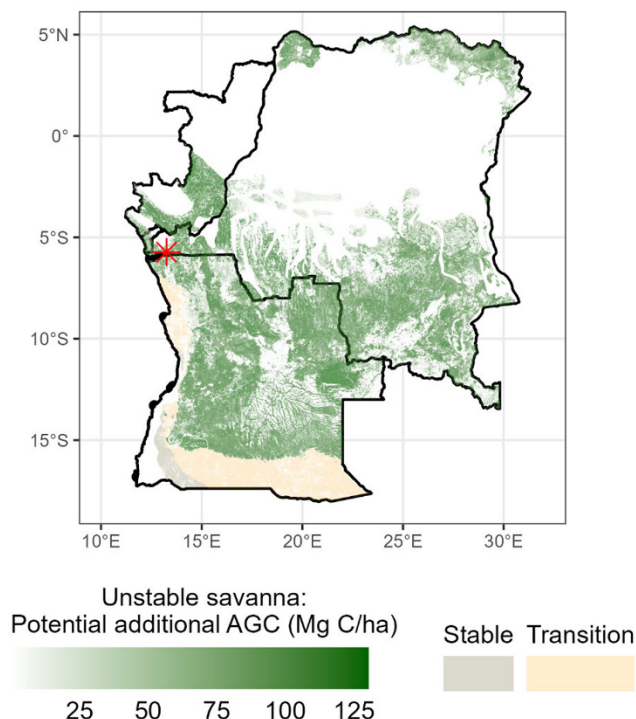


FIGURE 5 Potential additional aboveground carbon storage in unstable (mesic) savannas by 2100 in DR Congo, Congo and Angola. The fire exclusion experiment of Manzonzi in the DR Congo is indicated on the map with a red star. The presence of stable and transition savannas is shown as brown and yellow pixels. The uncertainty of the potential aboveground carbon storage is shown in [Figure S5](#). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 3 Country-level actual versus potential additional aboveground carbon (AGC, in Gt C) uptake by 2100 in unstable (mesic) artificial savannas. The uncertainty is indicated by the standard error.

Country	Area (Mha)	Actual AGC (Gt C)	Potential additional AGC (Gt C)
DR Congo	56.36	2 ± 1.38	5.38 ± 1.78
Angola	55.62	1.275 ± 0.77	5.98 ± 1.36
Congo	7.22	0.19 ± 0.14	0.763 ± 0.2
Total	119.2	3.45 ± 1.58	12.13 ± 2.25

where only $23.0 \pm 6.1 \text{ Mg C ha}^{-1}$ was stored after 60 years (Zhou et al., 2022), as compared to a predicted $98.14 \pm 22.8 \text{ Mg C ha}^{-1}$ in Manzonzi ([Figure 1b](#)). Differences in carbon recovery between Manzonzi and Kruger could be explained by water availability, which is one of the primary determinants of woody cover in savannas (King et al., 1997; Sankaran et al., 2005; Staver et al., 2009). Where Manzonzi receives a mean annual precipitation of $1180 \text{ mm year}^{-1}$ (Couralet, 2010; Deklerck et al., 2019; Ilondea et al., 2020), Kruger only receives 700 mm year^{-1} , which is within the transition zone between stable and unstable savannas ($516 \text{ mm/year} < \text{MAP} < 783 \text{ mm/year}$) (Sankaran et al., 2005; Staver et al., 2009).

Furthermore, proximity of seed bank reservoirs of forest specialist is also reported as an important condition for successful forest recovery (Chazdon, 2003; Deklerck et al., 2019; Jeltsch et al., 2000; King et al., 1997). With the old-growth rainforest of the Luki reserve at a distance of merely 5 km away from Manzonzi, the availability of seeds seems to be no limitation in our experiment. This is especially true for small-seeded tree species, which are dispersed through wind or small flying mammals and constitute more than 85% of the stems throughout the monitoring period ([Figure 3b](#)). However, large-seeded species requiring large-mammal dispersal are still scarce in Manzonzi (<5%), while they are an important group in the Luki OGF (54%) ([Figure 3b](#)). Recent research highlighted the role of megaherbivores, such as elephants, promoting higher AGC through browsing preferences and seed dispersal (Berzaghi et al., 2019, 2023). However, elephants and other large mammals disappeared decades ago from Manzonzi, which might significantly slow down the recovery of both carbon and species composition in the longer term.

4.2 | Rapid recovery of species richness versus slow recovery of species composition

Our results show that most biodiversity indices (Species richness, Simpson's index, Shannon index, Fisher's α) increased significantly over the 17-year monitoring period in Manzonzi ([Figure 2](#), [Table 1](#)). Yet, recovery of species composition representative of old-growth forest is much slower, owing to the rapid encroachment of short- and long-lived pioneer species that are typical for early succession stages and not for mature forest ([Figures 2 and 3](#)). Rapid recovery of biodiversity and species richness, combined with slow recovery of old-growth forest composition, was also reported in the large dataset of chronosequence studies of secondary regrowth forest in Neotropical regions (Poorter et al., 2016, 2021; Rozendaal et al., 2019), with 80% species richness recovery after 20 years versus only 34% species composition recovery after 20 years. Similar results were observed in a limited chronosequence dataset from the central Congo Basin (Makelele et al., 2021).

The Simpson index is a good indicator of secondary succession and community assembly because it is sensitive to the most abundant species and because, early in succession, the forest is dominated by just a few pioneer species (Kearsley, 2015). In our experiment, the Simpson index increased from 0.51 in the savanna control plots to 0.64 in the 2010 census of the Manzonzi regeneration experiment, to 0.80 in 2014 and finally to 0.83 in 2022 ([Table 1](#), [Table 2](#)). This rapid increase illustrates that the Manzonzi experiment is still in the early stages of forest succession. [Figure 3](#) confirms this, as the high numbers of both short- and long-lived pioneer species throughout the censuses, combined with the very few shade-tolerant species, show that the experiment is still in the initial pioneer stages of forest succession. However, [Figure 3](#) also shows that the experiment has already passed the stage where short-lived pioneers are dominant, as they are losing importance. The contrast between rapid recovery of aboveground carbon stocks and species

richness versus slow recovery of species composition is also visible on bivariate scatterplots (Figure 4). Finally, empirical observations and oral reports of villagers confirm that zoological biodiversity is also increasing. Multiple trees show signs of damage by bark-eating rodents (Figure S6).

Finally, Figure 3 confirms that the Luki plots truly represent old-growth forest, as only 17.5% of the trees belong to pioneer species (especially long-lived pioneers). Published radiocarbon dates on charcoal from top soils confirmed this, showing that the latest disturbance through fire at the investigated sites in Luki was 525 years ago (Hubau et al., 2013).

4.3 | Significant carbon–biodiversity relationships

Kendall's tau statistic showed a significant positive correlation ($p < .001$) between absolute AGC and species richness for each census period in Manzonzi (inset table in Figure 4a), which implies that for each census year, higher species richness corresponds to higher AGC stocks. In contrast, Kendall's tau statistic showed no significant correlation ($p = .622$) for the old-growth forest plot data of Luki, which suggests that there is no correlation between species richness and AGC stocks in old-growth forests. This observation is consistent with previous pan-tropical analysis of large plot datasets, which illustrated the absence of diversity–carbon relationships in old-growth tropical forests, while weak positive diversity–carbon relationships were reported at small spatial scales (0.04 ha plots) (Sullivan et al., 2017). This observation has implications for conservation strategies. Old-growth tropical forests can have any combination of tree diversity and carbon stocks, so both need to be considered when optimizing policies to manage tropical forests for carbon and biodiversity.

However, our results show that forest regeneration comes with the double benefit of rapid recovery of both carbon and species richness (Figure 4), suggesting that policy strategies based on natural forest regeneration result in both biodiversity and carbon gains. Our analysis shows that the baseline carbon storage and tree species diversity are low in unprotected periodically burned artificial savannas of our study region. These are almost exclusively situated in savanna specialist tree species, which almost entirely disappear from the system in the first few decades of forest regeneration (Figure 1; Table 1). We also quantify that forest specialist species, which start from near-zero in the baseline scenario, quickly recover carbon stocks (6.57% of OGF aboveground carbon stocks after 17 years) and species richness (33.17% of OGF species richness after 17 years) after fire protection is initiated.

4.4 | Nature-based solution

The success of both carbon (Figure 1) and species richness (Figure 2) recovery in Manzonzi illustrates the potential power of a simple management tool. Protection of artificial unstable savannas does

require logistical efforts, but the rest of the process is very cost- and labour-efficient, as the actual job is done by the natural process of forest succession. Recent analysis also showed that natural forest restoration has an average carbon storage capacity that is six times higher compared to agroforestry and 40 times more than that of tree plantations for forest carbon sequestration (Lewis et al., 2019). Therefore, in contrast to other forms of landscape restoration, natural forest regeneration remains the most successful, cheapest and least technical option for large-scale biodiversity and carbon recovery and is widely recognized as a major NBS to both mitigate global climate change and fight biodiversity loss (Girardin et al., 2021; Higgins et al., 2007; Löfqvist et al., 2023; Moreira, 2000; Seddon et al., 2020; Suding et al., 2015). Furthermore, while there is much uncertainty on the total suitable and available land for forest restoration and on the potential additional carbon recovery on these lands, scientific studies agree that abundant (up to three-quarters) suitable and available land can be found in the tropics (Abreu et al., 2017; Bastin et al., 2019; Laestadius et al., 2011; Lewis et al., 2019).

The increasing focus on forest restoration as a NBS to the global climate and biodiversity crises led to ambitious targets for ecosystem restoration initiatives at national, regional and global levels (Strassburg et al., 2020; Suding et al., 2015). Specifically, the African Forest Landscape Restoration Initiative (AFR100) is a country-led effort to restore 100 million hectares of land in Africa by 2030. Forest restoration initiatives facilitate the recovery process of carbon storage, biodiversity and other ecosystem services (Suding et al., 2015).

The success of these initiatives largely depends on the engagement of rural populations, who often reside close to restorable land, with one-third living within 8 km of such areas (Erbaugh et al., 2020). As a result, forest restoration through NBS not only provides environmental benefits but also offers significant advantages to local communities. These include deriving income from the sale of carbon credits to help communities adapt to climatic or other environmental shocks or be used for local development purposes (Erbaugh et al., 2020; Löfqvist et al., 2023; Seddon et al., 2020). Such economic incentives can encourage participation in forest restoration, especially if local populations are effectively integrated into these programs and receive financial support through Payment for Ecosystem Services (PES) (Lamb et al., 2005; Löfqvist et al., 2023; Suding et al., 2015). Beyond the financial gains from carbon credits, successful forest restoration can integrate with the rural lifestyles of local communities in terms of food production systems, farming, shifting cultivation, hunting and access to forest resources like fruits, nuts, fuel, honey and building materials (Seddon et al., 2020). This integration, crucial for long-term success, requires the sensitization of communities to the importance and benefits of NBS to ensure their willing participation and tangible benefits. Therefore, incorporating indigenous knowledge, such as the role of mammalian seed dispersers in ecosystem functions, can enhance conservation strategies, making them more likely to be adopted and successful.

Additionally, forest restoration can alleviate pressure on the limited natural forests in national parks and reserves across central Africa by providing alternative sources for forest products,

potentially reducing activities like wildlife poaching and timber collection. Restored forests, particularly those adjacent to existing forest reserves, can extend ecosystem functionality by offering expanded habitats, buffering from human communities and supporting more intact carbon and water cycling processes.

On a critical note, policymakers should bear in mind that reforestation in tropical savannas might also lead to some biodiversity loss (Abreu et al., 2017). Recent analysis showed that savannas are floristically impoverished, as our data suggest, but transition zones do hold high evolutionary diversity and serve as evolutionary cross-roads (Rees et al., 2023).

4.5 | Bottlenecks and uncertainties

There are considerable bottlenecks to the success of restoration initiatives. Although the growing number of commitments is encouraging, they remain political actions made in a 'top-down' instead of 'bottom-up' manner, without any real quantification and localization of the pledged areas. Some countries seem to be overambitious, pledging more land than is suitable or available (Bastin et al., 2019). Other countries are under-ambitious, pledging only a small fraction of suitable or available land. DR Congo pledged 8Mha under AFR100, while we showed that it has 56.36Mha of unstable savanna with restoration potential (Figure 5; Table 3). Congo pledged 2Mha, whereas we show that it has 7.22Mha of unstable savannas. Angola is not even part of the AFR100 initiative, while it has 55.62Mha of unstable savannas.

Another bottleneck is the uncertainty of the suitability of land and the long-term pathways of carbon and biodiversity recovery. Using very different remote sensing approaches, two independent studies reported between 0.9 and 2.0 billion hectares of restorable land globally (Bastin et al., 2019; Laestadius et al., 2011). Long-term carbon recovery trajectories are even more difficult to quantify (Maurent et al., 2023). Carbon additions depend on many factors, such as initial carbon stocks, resource availability (soil and water), proximity of seed sources, prior land history and climate (King et al., 1997; Sankaran et al., 2005). Particularly shifting climate conditions will likely have an impact on the availability of suitable land for forest restoration in the coming decades, while projections of restoration success often don't account for this (Bastin et al., 2019; Koch & Kaplan, 2022).

A major source of uncertainty is the lack of ground-based monitoring of forest recovery. Although a substantial dataset is available to monitor the recovery potential of secondary forests in Neotropical regions (Chazdon et al., 2016; Rozendaal et al., 2022), only a handful of plots are available in central African forests (Bauters et al., 2019; Makelele et al., 2021). Furthermore, these studies are based on chronosequences rather than on long-term repeated measurements of regenerating forest plots (Chazdon, 2003). Forest recovery in chronosequences is estimated indirectly using a space-for-time approach and based on the assumption that the same successional process takes place within each stand (Chazdon

et al., 2006; Poorter et al., 2021). Chronosequence studies often include sites that are regenerating shortly after disturbance, leaving no time for savanna vegetation establishment. As such, they might not be representative of the regeneration of areas that were converted to artificial unstable savannas decades ago. Our results show that initial recovery rates in artificial savannas might be slower than in chronosequences, as illustrated by the Gompertz model, which performs better than the exponential model that fits well with chronosequence data (Figure S3). Long-term fire exclusion experiments are extremely rare in Africa. Substantial efforts were done in Ghana (Swaine et al., 1992), Gabon (King et al., 1997) and South Africa (Zhou et al., 2022), but apart from our experiment, we found no published reference for the three central African countries surrounding our study site (Figure 5). This limits the robust upscaling of total potential carbon uptake, as there is much uncertainty on the influence of several parameters such as rainfall, soil fertility, prior vegetation, land-use history and surrounding forest cover. Furthermore, very little research has been conducted on the evolution of soil carbon stocks, which might change substantially during forest recovery on artificial savannas (Zhou et al., 2023).

Despite bottlenecks and uncertainties, existing predictions are promising. We estimate a total potential additional recovery of $12.13 \pm 2.25 \text{ Gt C}$ if all 119.2Mha of unstable savannas in DR Congo, Congo and Angola are pledged and protected from disturbance (Figure 5; Table 3). This is comparable to the predicted 42 Gt C that would be additionally stored by 2100 if the targeted 350Mha of the Bonn Challenge were restored to natural forest (and not to agroforestry or tree plantations) (Lewis et al., 2019). Our predicted $12.13 \pm 2.25 \text{ Gt C}$ by 2100 would already account for more than one-fifth of the uptake needed in forests to keep global warming below 1.5°C, as projected by the pathways of the IPCC (2018). We do emphasize, however, that our predictions of total carbon uptake are based on assumptions. We applied the same recovery trajectory (Figure 1) throughout our study area (Figure 5), while actual recovery is most likely different among regions and even specific locations. Furthermore, our predictions do not account for future climate change, which might stabilize some of the present-day unstable savannas (Bastin et al., 2019; Koch & Kaplan, 2022).

5 | CONCLUSION

The fire exclusion experiment in the artificial unstable savanna of Manzonzi shows rapid recovery of both carbon stocks and species richness, with a rapid increase in the stem density of pioneer forest species. This illustrates that natural forest regeneration is a successful NBS to both mitigate global climate change and fight biodiversity loss. It comes with the advantage of additional benefits like a healthy water balance, the production of forest products that can be used by local communities and reduction of pressure on remaining intact forests. Furthermore, natural forest regeneration is a cheap and simple management strategy. However, upscaling this management within the framework of global or regional initiatives (e.g.

AFR100) is constrained due to uncertainties of the suitability of land and uncertainties on the long-term pathways of carbon and biodiversity recovery. Therefore, more ground-based in situ monitoring is needed to improve predictions of the benefits of large-scale restoration initiatives and to quantify variation due to resource availability (e.g. rainfall and soil fertility), prior vegetation, changes in soil carbon stocks, land-use history and surrounding forest cover. Finally, we also show that the recovery of species composition representative of old-growth forests is slow, with an estimated 90% recovery after 124 ± 3 years. This illustrates that global protection of intact rainforest is still of paramount importance to avoid further biodiversity loss.

AUTHOR CONTRIBUTIONS

Brice Yannick Djiofack: Data curation; formal analysis; methodology; software; visualization; writing – original draft; writing – review and editing. **Hans Beeckman:** Conceptualization; funding acquisition; supervision; validation; writing – review and editing. **Nils Bourland:** Supervision; validation; writing – review and editing. **Basile Luse Belanganayi:** Data curation; writing – review and editing. **Félix Laurent:** Data curation; project administration; writing – review and editing. **Bhely Angoboy Ilondea:** Conceptualization; data curation; writing – review and editing. **Laurent Nsenga:** Conceptualization; writing – review and editing. **Victor Deklerck:** Data curation; writing – review and editing. **Alain Huart:** Conceptualization; writing – review and editing. **Menard Mbende Longwwango:** Conceptualization; writing – review and editing. **Geert Lejeune:** Conceptualization; writing – review and editing. **Joris Van Acker:** Validation; writing – review and editing. **William W. M. Verbiest:** Formal analysis; methodology; software; visualization; writing – original draft; writing – review and editing. **Jan Van den Bulcke:** Validation; writing – review and editing. **Tom De Mil:** Validation; writing – review and editing. **Wannes Hubau:** Conceptualization; methodology; software; supervision; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.24221323>, reference number 24221323.

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REFERENCES

- Abreu, R. C. R., Hoffmann, W. A., Vasconcelos, H. L., Pilon, N. A., Rossatto, D. R., & Durigan, G. (2017). The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances*, 3(8), e1701284. <https://doi.org/10.1126/sciadv.1701284>
- African Plant Database. (2023). <https://africanplantdatabase.ch/en/nomen/10195>
- Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S. L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T. R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemirńska, K., Phillips, O. L., & Oliveras, I. (2020). Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. *Nature Communications*, 11, 3346. <https://doi.org/10.1038/s41467-020-16973-4>
- Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., & Marcano-Vega, H. (2000). Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Restoration Ecology*, 8(4), 328–338. <https://doi.org/10.1046/j.1526-100x.2000.80048.x>
- Avitabile, V., Herold, M., Heuvelink, G. B. M., Lewis, S. L., Phillips, O. L., Asner, G. P., Armston, J., Ashton, P. S., Banin, L., Bayol, N., Berry, N. J., Boeckx, P., de Jong, B. H. J., Devries, B., Girardin, C. A. J., Kearsley, E., Lindsell, J. A., Lopez-Gonzalez, G., Lucas, R., ... Willcock, S. (2016). An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology*, 22(4), 1406–1420. <https://doi.org/10.1111/GCB.13139>
- Baccini, A., & Asner, G. P. (2014). Improving pantropical forest carbon maps with airborne LiDAR sampling. *Carbon Management*, 4(6), 591–600. <https://doi.org/10.4155/CMT.13.66>
- Bastin, J. F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., & Crowther, T. W. (2019). The global tree restoration potential. *Science*, 364(6448), 76–79. <https://doi.org/10.1126/science.aax0848>
- Bauters, M., Vercleyen, O., Vanlauwe, B., Six, J., Bonyoma, B., Badjoko, H., Hubau, W., Hoyt, A., Boudin, M., Verbeeck, H., & Boeckx, P. (2019). Long-term recovery of the functional community assembly and carbon pools in an African tropical forest succession. *Biotropica*, 51(3), 319–329. <https://doi.org/10.1111/btp.12647>
- Bennett, A. C., Dargie, G. C., Cuni-Sanchez, A., Mukendi, J. T., Hubau, W., Mukinzi, J. M., Phillips, O. L., Malhi, Y., Sullivan, M. J. P., Cooper, D. L. M., Adu-Bredu, S., Affum-Baffoe, K., Amani, C. A., Banin, L. F., Beeckman, H., Begne, S. K., Bocko, Y. E., Boeckx, P., Bogaert, J., ... Lewis, S. L. (2021). Resistance of African tropical forests to an extreme climate anomaly. *Proceedings of the National Academy*

- of *Sciences of the United States of America*, 118(21), e2003169118. <https://doi.org/10.1073/pnas.2003169118>
- Berzaghi, F., Bretagnolle, F., Durand-Bessart, C., & Blake, S. (2023). Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. *Proceedings of the National Academy of Sciences of the United States of America*, 120(5), e2201832120. <https://doi.org/10.1073/pnas.2201832120>
- Berzaghi, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., Scaranello, M., Scarascia-Mugnozza, G., & Doughty, C. E. (2019). Carbon stocks in central African forests enhanced by elephant disturbance. *Nature Geoscience*, 12(9), 725–729. <https://doi.org/10.1038/s41561-019-0395-6>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20(10), 3177–3190. <https://doi.org/10.1111/gcb.12629>
- Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1), 51–71. <https://doi.org/10.1078/1433-8319-00042>
- Chazdon, R. L., Broadbent, E. N., Rozendaal, D. M. A., Bongers, F., Zambrano, A. M. A., Aide, T. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Craven, D., Almeida-Cortez, J. S., Cabral, G. A. L., de Jong, B., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Poorter, L. (2016). Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances*, 2(5), e1501639. <https://doi.org/10.1126/sciadv.1501639>
- Chazdon, R. L., Letcher, S. G., van Breugel, M., Martínez-Ramos, M., Bongers, F., & Finegan, B. (2006). Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society B*, 362, 273–289. <https://doi.org/10.1098/rstb.2006.1990>
- Compère, P. (1970). Carte des sols et de la végétation du Congo Belge et du Ruanda-Urundi: 25. Bas-Congo. Notice Explicative. Bruxelles: Publications de l'Institut National Pour l'Etude Agronomique Du Congo Belge (INEAC).
- Coualet, C. (2010). *Community dynamics, phenology and growth of tropical trees in the rain forest reserve of Luki, Democratic Republic of Congo*. PhD thesis (p. 173). Faculty of Bioscience Engineering, Ghent University. <http://hdl.handle.net/1854/LU-1028918>
- Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Science*, 361(6407), 1108–1111. <https://doi.org/10.1126/science.aau3445>
- Deklerck, V., De Mil, T., Ilondea, B. A., Nsenga, L., De Caluwé, C., Van den Bulcke, J., Van Acker, J., Beeckman, H., & Hubau, W. (2019). Rate of forest recovery after fire exclusion on anthropogenic savannas in the Democratic Republic of Congo. *Biological Conservation*, 233, 118–130. <https://doi.org/10.1016/j.biocon.2019.02.027>
- Donis, C. (1948). *Essai d'économie forestière au Mayumbe*. Institut national pour l'étude agronomique du Congo belge.
- Doucet, J.-L. (2003). *L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon*. Université de Liège—Faculté des Sciences agronomiques de Gembloux. <http://orbi.ulg.ac.be/handle/2268/22451>
- Erb, K. H., Kastner, T., Plutzer, C., Bais, A. L. S., Carvalhais, N., Fetzl, T., Gingrich, S., Haberl, H., Lauk, C., Niedertscheider, M., Pongratz, J., Thurner, M., & Luyssaert, S. (2018). Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature*, 553(7686), 73–76. <https://doi.org/10.1038/nature25138>
- Erbaugh, J. T., Pradhan, N., Adams, J., Oldekop, J. A., Agrawal, A., Brockington, D., Pritchard, R., & Chhatre, A. (2020). Global forest restoration and the importance of prioritizing local communities. *Nature Ecology & Evolution*, 4(11), 1472–1476. <https://doi.org/10.1038/s41559-020-01282-2>
- Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L., Quesada, C. a., Affum-Baffoe, K., Arets, E. J. M. M., Berry, N. J., Bird, M., Brondizio, E. S., de Camargo, P., Chave, J., Djangbletey, G., Domingues, T. F., Drescher, M., Fearnside, P. M., França, M. B., Fyllas, N. M., ... Lloyd, J. (2011). Height-diameter allometry of tropical forest trees. *Biogeosciences*, 8(5), 1081–1106. <https://doi.org/10.5194/bg-8-1081-2011>
- Fisher, J. B., Sikka, M., Sitch, S., Ciais, P., Poulter, B., Galbraith, D., Lee, J.-E. E., Huntingford, C., Viovy, N., Zeng, N., Ahlström, A., Lomas, M. R., Levy, P. E., Frankenberg, C., Saatchi, S., & Malhi, Y. (2013). African tropical rainforest net carbon dioxide fluxes in the twentieth century. *Philosophical Transactions of the Royal Society B*, 368, 20120376. <https://doi.org/10.1098/rstb.2012.0376>
- ForestPlots.net, Blundo, C., Carilla, J., Grau, R., Malizia, A., Malizia, L., Osinaga-Acosta, O., Bird, M., Bradford, M., Catchpole, D., Ford, A., Graham, A., Hilbert, D., Kemp, J., Laurance, S., Laurance, W., Ishida, F. Y., Marshall, A., Waite, C., ... Tran, H. D. (2021). Taking the pulse of Earth's tropical forests using networks of highly distributed plots. *Biological Conservation*, 260, 108849. <https://doi.org/10.1016/j.biocon.2020.108849>
- Friedlingstein, P., Allen, M., Canadell, J. G., Peters, G. P., & Seneviratne, S. I. (2019). Comment on "The global tree restoration potential". *Science*, 366(6463), 76–79. <https://doi.org/10.1126/science.aay8060>
- Gerland, P., Raftery, A. E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B. K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G. K., & Wilmoth, J. (2014). World population stabilization unlikely this century. *Science*, 320(6), 234–237. <https://doi.org/10.1126/science.1257469>
- Girardin, C. A. J., Jenkins, S., Seddon, N., Allen, M., Lewis, S. L., Wheeler, C. E., Griscom, B. W., & Malhi, Y. (2021). Nature-based solutions can help cool the planet—If we act now. *Nature*, 593(7858), 191–194. <https://doi.org/10.1038/d41586-021-01241-2>
- Harper, K. L., Lamarche, C., Hartley, A., Peylin, P., Ottlé, C., Bastrikov, V., San Martín, R., Bohnenstengel, S. I., Kirches, G., Boettcher, M., Shevchuk, R., Brockmann, C., & Defourny, P. (2023). A 29-year time series of annual 300m resolution plant-functional-type maps for climate models. *Earth System Science Data*, 15(3), 1465–1499. <https://doi.org/10.5194/ESSD-15-1465-2023>
- Hawthorne, W. D. (1995). *Ecological profiles of Ghanaian forest trees tropical forestry paper 29*. Oxford Forestry Institute, Department of Plant Sciences.
- Heinrich, V. H. A., Vancutsem, C., Dalagnol, R., Rosan, T. M., Fawcett, D., Silva-Junior, C. H. L., Cassol, H. L. G., Achard, F., Jucker, T., Silva, C. A., House, J., Sitch, S., Hales, T. C., & Aragão, L. E. O. C. (2023). The carbon sink of secondary and degraded humid tropical forests. *Nature*, 615(7952), 436–442. <https://doi.org/10.1038/s41586-022-05679-w>
- Higgins, S. I., William, J. B., Edmund, F. C., Bronn, A., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin, B., Governder, N., Rademan, L., O'Regan, S., Potgieter, A. L. F., Scheiter, S., Sowry, R., Trollope, L., & Trollope, W. S. W. (2007). Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, 88(5), 1119–1125. <https://doi.org/10.1890/06-1664>
- Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sánchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland,

- T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., ... Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, 579(7797), 80–87. <https://doi.org/10.1038/s41586-020-2035-0>
- Hubau, W., Van den Bulcke, J., Kitin, P., Mees, F., Baert, G., Verschuren, D., Nsenga, L., Van Acker, J., & Beeckman, H. (2013). Ancient charcoal as a natural archive for paleofire regime and vegetation change in the Mayumbe, Democratic Republic of the Congo. *Quaternary Research*, 80(2), 326–340. <https://doi.org/10.1016/j.yqres.2013.04.006>
- Hubau, W., Van den Bulcke, J., Van Acker, J., & Beeckman, H. (2015). Charcoal-inferred Holocene fire and vegetation history linked to drought periods in the Democratic Republic of Congo. *Global Change Biology*, 21(6), 2296–2308. <https://doi.org/10.1111/gcb.12844>
- Ilonde, A. B., De Mil, T., Hubau, W., Van Acker, J., Van den Bulcke, J., Fayolle, A., Bourland, N., Kapalay, O., Chantain, A., Ewango, C., & Beeckman, H. (2020). Towards improving the assessment of rain-forest carbon: Complementary evidence from repeated diameter measurements and dated wood. *Dendrochronologia*, 62, 125723. <https://doi.org/10.1016/j.dendro.2020.125723>
- IPCC. (2018). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & T. Waterfield (Eds.), *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* (pp. 3–24). Cambridge University Press. <https://doi.org/10.1017/9781009157940.001>
- Jeltsch, F., Weber, G. E., & Grimm, V. (2000). Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass co-existence. *Plant Ecology*, 150(1–2), 161–171. <https://doi.org/10.1023/A:1026590806682>
- Jung, M., Arnell, A., de Lamo, X., García-Rangel, S., Lewis, M., Mark, J., Merow, C., Miles, L., Ondo, I., Pironon, S., Ravillious, C., Rivers, M., Schepashenko, D., Tallowin, O., van Soesbergen, A., Govaerts, R., Boyle, B. L., Enquist, B. J., Feng, X., ... Visconti, P. (2021). Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nature Ecology and Evolution*, 5, 1499–1509. <https://doi.org/10.1038/s41559-021-01528-7>
- Karger, D. N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. <https://doi.org/10.1038/sdata.2017.122>
- Kearsley, E. (2015). *Carbon storage and functional diversity of tropical rain-forest in The Congo Basin*. PhD thesis (p. 199). Faculty of Bioscience Engineering, Ghent University. <http://hdl.handle.net/1854/LU-6901138>
- King, J., Moutsinga, J.-B., & Doufoulon, G. (1997). Conversion of anthropogenic savanna to production forest through fire-protection of the forest-savanna edge in Gabon, Central Africa. *Forest Ecology and Management*, 94(1), 233–247. [https://doi.org/10.1016/S0378-1127\(96\)03925-4](https://doi.org/10.1016/S0378-1127(96)03925-4)
- Koch, A., & Kaplan, J. O. (2022). Tropical forest restoration under future climate change. *Nature Climate Change*, 12(3), 279–283. <https://doi.org/10.1038/s41558-022-01289-6>
- Laestadius, L., Maginnis, S., Minnemeyer, S., & Potapov, P. (2011). Mapping opportunities for forest landscape restoration. www.wri.org/restoringforests
- Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science*, 310(5754), 1628–1632. <https://doi.org/10.1126/science.1111773>
- Lebrun, J., & Gilbert, G. (1954). *Une classification écologique des forêts du Congo*. Publications de l'INEAC. INEAC.
- Lewis, S. L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T. R., Ojo, L. O., Phillips, O. L., Reitsma, J. M., White, L., & Comiskey, J. A. (2009). Increasing carbon storage in intact African tropical forests. *Nature*, 457(7232), 1003–1006. <https://doi.org/10.1038/nature07771>
- Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., van der Heijden, G. M. F., Phillips, O. L., Affum-Baffoe, K., Baker, T. R., Banin, L., Bastin, J.-F., Beeckman, H., Boeckx, P., Bogaert, J., De Cannière, C., Chezeaux, E., Clark, C. J., Collins, M., Djangbletey, G., ... Zemagho, L. (2013). Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B*, 368, 20120295. <https://doi.org/10.1098/rstb.2012.0295>
- Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A., & Koch, A. (2019). Regenerate natural forests to store carbon. *Nature*, 568, 25–28. <https://doi.org/10.1038/d41586-019-01026-8>
- Liang, J., Gamarra, J. G. P., Picard, N., Zhou, M., Pijanowski, B., Jacobs, D. F., Reich, P. B., Crowther, T. W., Nabuurs, G.-J., De-Miguel, S., Fang, J., Woodall, C. W., Svenning, J.-C., Jucker, T., Bastin, J.-F., Wiser, S. K., Slik, F., Hérault, B., Alberti, G., ... Hui, C. (2022). Co-limitation towards lower latitudes shapes global forest diversity gradients. *Nature Ecology & Evolution*, 6(10), 1423–1437. <https://doi.org/10.1038/s41559-022-01831-x>
- Library, W. O., Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(2), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Löfqvist, S., Garrett, R. D., & Ghazoul, J. (2023). Incentives and barriers to private finance for forest and landscape restoration. *Nature Ecology & Evolution*, 7, 707–715. <https://doi.org/10.1038/s41559-023-02037-5>
- Lubini, A. (1997). *La végétation de la Réserve de biosphère de Luki au Mayombe (Zaire)* (Vol. 10). Jardin Botanique National de Belgique.
- Mailund, T. (2019). Manipulating data frames: dplyr. In T. Mailund (Ed.), *R data science quick reference: A pocket guide to APIs, libraries, and packages* (pp. 109–160). Apress. https://doi.org/10.1007/978-1-4842-4894-2_7
- Makelele, I. A., Verheyen, K., Boeckx, P., Cizungu Ntaboba, L., Mujinya Bazirake, B., Ewango, C., & Bauters, M. (2021). Afrotropical secondary forests exhibit fast diversity and functional recovery, but slow compositional and carbon recovery after shifting cultivation. *Journal of Vegetation Science*, 32(5), e13071. <https://doi.org/10.1111/jvs.13071>
- Marcon, E. (2015). *Mesures de la Biodiversité*. AgroParisTech. <https://hal-agroparistech.archives-ouvertes.fr/cel-01205813>
- Martin, A. R., Doraisami, M., & Thomas, S. C. (2018). Global patterns in wood carbon concentration across the world's trees and forests. *Nature Geoscience*, 11(12), 915–920. <https://doi.org/10.1038/s41561-018-0246-x>
- Maurent, E., Hérault, B., Pioniot, C., Derroire, G., Delgado, D., Finegan, B., Kientz, M. A., Amani, B. H. K., & Bieng, M. A. N. (2023). A common framework to model recovery in disturbed tropical forests. *Ecological Modelling*, 483, 110418. <https://doi.org/10.1016/j.ecolm.2023.110418>
- Meunier, Q., Mombogou, C., & Doucet, J.-L. (2015). *Les arbres utiles du Gabon*. Presses Agronomiques de Gembloux. <http://hdl.handle.net/2268/183815>
- Mitchard, E. T. A. (2018). The tropical forest carbon cycle and climate change. *Nature*, 559(7715), 527–534. <https://doi.org/10.1038/s41586-018-0300-2>
- Mitchard, E. T. A., Saatchi, S. S., Baccini, A., Asner, G. P., Goetz, S. J., Harris, N. L., & Brown, S. (2013). Uncertainty in the spatial distribution of tropical forest biomass: A comparison of pan-tropical maps.

- Carbon Balance and Management*, 8(1), 1–13. <https://doi.org/10.1186/1750-0680-8-10>
- Moreira, A. G. (2000). Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography*, 27(4), 1021–1029. <https://doi.org/10.1046/j.1365-2699.2000.00422.x>
- Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S. A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., & Rillig, M. C. (2014). Choosing and using diversity indices: Insights for ecological applications from the German biodiversity Exploratories. *Ecology and Evolution*, 4(18), 3514–3524. <https://doi.org/10.1002/ece3.1155>
- Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., & Lehmann, C. E. R. (2018). Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*, 220(1), 10–24. <https://doi.org/10.1111/NPH.15236>
- Ostertagová, E., Ostertag, O., & Kováč, J. (2014). Methodology and application of the Kruskal–Wallis test. *Applied Mechanics and Materials*, 611, 115–120. <https://doi.org/10.4028/www.scientific.net/AMM.611.115>
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., de Almeida-Cortez, J. S., Cabral, G. A. L., De Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, 530(7589), 211–214. <https://doi.org/10.1038/nature16512>
- Poorter, L., Craven, D., Jakovac, C. C., van der Sande, M. T., Amissah, L., Bongers, F., Chazdon, R. L., Farrior, C. E., Kambach, S., Meave, J. A., Muñoz, R., Norden, N., Rüger, N., van Breugel, M., Almeyda Zambrano, A. M., Amani, B., Andrade, J. L., Brancalion, P. H. S., Broadbent, E. N., ... Hérault, B. (2021). Multidimensional tropical forest recovery. *Science*, 374(6573), 1370–1376. <https://doi.org/10.1126/science.abh3629>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R foundation for statistical computing.
- Rees, M., Godlee, J. L., Harris, D. J., Ryan, C. M., & Dexter, K. G. (2023). Testing White's floristic impoverishment hypothesis in the forest-savanna transition zones of Africa. *Diversity*, 15(7), 833. <https://doi.org/10.3390/d15070833>
- Rozendaal, D. M. A., Bongers, F., Aide, T. M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J. M., Bentos, T. V., Brancalion, P. H. S., Cabral, G. A. L., Calvo-Rodriguez, S., Chave, J., César, R. G., Chazdon, R. L., Condit, R., Dalling, J. S., de Almeida-Cortez, J. S., de Jong, B., de Oliveira, A., ... Poorter, L. (2019). Biodiversity recovery of Neotropical secondary forests. *Science Advances*, 5(3), eaau3114. <https://doi.org/10.1126/sciadv.aau3114>
- Rozendaal, D. M. A., & Chazdon, R. L. (2015). Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. *Ecological Applications*, 25(2), 506–516. <https://doi.org/10.1890/14-0054.1>
- Rozendaal, D. M. A., Suarez, D. R., De Sy, V., Avitabile, V., Carter, S., Yao, C. Y. A., Alvarez-Davila, E., Anderson-Teixeira, K., Araujo-Murakami, A., Arroyo, L., Barca, B., Baker, T. R., Birgazzi, L., Bongers, F., Branthomme, A., Brienen, R. J. W., Carreiras, J. M. B., Gatti, R. C., Cook-Patton, S. C., ... Herold, M. (2022). Aboveground forest biomass varies across continents, ecological zones and successional stages: Refined IPCC default values for tropical and subtropical forests. *Environmental Research Letters*, 17(1), 14047. <https://doi.org/10.1088/1748-9326/ac45b3>
- Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R., Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M., & Morel, A. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*, 108(24), 9899–9904. <https://doi.org/10.1073/pnas.1019576108>
- San Jose, J. J., & Farinas, M. R. (1983). Changes in tree density and species composition in a protected Trachypogon Savanna, Venezuela. *Ecology*, 64(3), 447–453. <https://doi.org/10.2307/1939963>
- San Jose, J. J., Montes, R. A., & Fariñas, M. R. (1998). Carbon stocks and fluxes in a temporal scaling from a savanna to a semi-deciduous forest. *Forest Ecology and Management*, 105(1), 251–262. [https://doi.org/10.1016/S0378-1127\(97\)00288-0](https://doi.org/10.1016/S0378-1127(97)00288-0)
- Sankaran, M. (2019). Droughts and the ecological future of tropical savanna vegetation. *Journal of Ecology*, 107(4), 1531–1549. <https://doi.org/10.1111/1365-2745.13195>
- Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., ... Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, 438(7069), 846–849. <https://doi.org/10.1038/nature04070>
- Seddon, N., Chausson, A., Berry, P., Girardin, C. A. J., Smith, A., & Turner, B. (2020). Understanding the value and limits of nature-based solutions to climate change and other global challenges. *Philosophical Transactions of the Royal Society B*, 375(1794), 20190120. <https://doi.org/10.1098/rstb.2019.0120>
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27(3), 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- Silva, L. C. R., Hoffmann, W. A., Rossatto, D. R., Haridasan, M., Franco, A. C., & Horwath, W. R. (2013). Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. *Plant and Soil*, 373(1), 829–842. <https://doi.org/10.1007/s11104-013-1822-x>
- Simpson, E. H. (1949). Measurement of diversity. *Nature*, 163(688), 688. <https://doi.org/10.1038/163688a0>
- Spawn, S. A., Sullivan, C. C., Lark, T. J., & Gibbs, H. K. (2020). Harmonized global maps of above and belowground biomass carbon density in the year 2010. *Scientific Data*, 7(1), 1–22. <https://doi.org/10.1038/s41597-020-0444-4>
- Staver, A. C., Archibald, S., & Levin, S. A. (2011). The global extent and determinants of savanna and forest as alternative biome states. *Science*, 334(6053), 230–232. <https://doi.org/10.1126/science.1210465>
- Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J., & Waldram, M. S. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19(7), 1909–1919. <https://doi.org/10.1890/08-1907.1>
- Strassburg, B. B. N., Iribarrem, A., Beyer, H. L., Cordeiro, C. L., Crouzeilles, R., Jakovac, C. C., Braga Junqueira, A., Lacerda, E., Latawiec, A. E., Balmford, A., Brooks, T. M., Butchart, S. H. M., Chazdon, R. L., Erb, K. H., Brancalion, P., Buchanan, G., Cooper, D., Díaz, S., Donald, P. F., ... Visconti, P. (2020). Global priority areas for ecosystem restoration. *Nature*, 586, 724–729. <https://doi.org/10.1038/s41586-020-2784-9>
- Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B., & Schwartz, K. Z. S. (2015). Committing to ecological restoration: Efforts around the globe need legal and policy clarification. *Science*, 348(6235), 638–640.
- Sullivan, M. J. P., Lewis, S. L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A. C., Ewango, C. E. N., Hubau, W., Marimon, B., Monteagudo-Mendoza, A., Qie, L., Sonké, B., Martinez, R. V., Baker, T. R., Brienen, R. J. W., Feldpausch, T. R., Galbraith, D., Gloor, M., Malhi, Y., ... Phillips, O. L. (2020). Long-term thermal sensitivity of Earth's tropical forests. *Science*, 368(6493), 869–874. <https://doi.org/10.1126/science.aaw7578>
- Sullivan, M. J. P., Talbot, J., Lewis, S. L., Phillips, O. L., Qie, L., Begne, S. K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles,

- L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., Ter Steege, H., White, L. J. T., Affum-Baffoe, K., Aiba, S. I., De Almeida, E. C., ... Zemagho, L. (2017). Diversity and carbon storage across the tropical forest biome. *Scientific Reports*, 7(1), 39102. <https://doi.org/10.1038/srep39102>
- Swaine, M. D., Hawthorne, W. D., & Ogle, T. K. (1992). The effects of fire exclusion on savanna vegetation at Kpong, Ghana. *Biotropica*, 24(2), 166–172. <https://doi.org/10.2307/2388670>
- Taylor, J. M. G. (1987). Kendall's and Spearman's correlation coefficients in the presence of a blocking variable. *Biometrics*, 43(2), 409. <https://doi.org/10.2307/2531822>
- Toussaint, L., Wilczek, R., Gillett, J. B., & Boutique, R. (1953). *Flore du Congo Belge et du Ruanda-Urundi: Papilionaceae (Sophoreae, Genisteae, Trifolieae et Loteae)* (Vol. IV). INEAC.
- Tyukavina, A., Hansen, M. C., Potapov, P., Parker, D., Okpa, C., Stehman, S. V., Kommareddy, I., & Turubanova, S. (2018). Congo Basin forest loss dominated by increasing smallholder clearing. *Science Advances*, 4(11), 2993. <https://doi.org/10.1126/sciadv.aat2993>
- Valentini, R., Arneth, A., Bombelli, A., Castaldi, S., Cazzolla Gatti, R., Chevallier, F., Ciais, P., Grieco, E., Hartmann, J., Henry, M., Houghton, R. A., Jung, M., Kutsch, W. L., Malhi, Y., Mayorga, E., Merbold, L., Murray-Tortarolo, G., Papale, D., Peylin, P., ... Scholes, R. J. (2014). A full greenhouse gases budget of Africa: Synthesis, uncertainties, and vulnerabilities. *Biogeosciences*, 11(2), 381–407. <https://doi.org/10.5194/bg-11-381-2014>
- Van Der Werf, G. R., Randerson, J. T., Giglio, L., Van Leeuwen, T. T., Chen, Y., Rogers, B. M., Mu, M., Van Marle, M. J. E., Morton, D. C., Collatz, G. J., Yokelson, R. J., & Kasibhatla, P. S. (2017). Global fire emissions estimates during 1997–2016. *Earth System Science Data*, 9(2), 697–720. <https://doi.org/10.5194/essd-9-697-2017>
- White, F. (1983). *The vegetation of Africa*. UNESCO.
- White, L. J. T., Masudi, E. B., Ndongo, J. D., Matondo, R., Soudan-Nonault, A., Ngomanda, A., Averti, I. S., Ewango, C. E. N., Sonké, B., & Lewis, S. L. (2021). Congo Basin rainforest—Invest US\$150 million in science. *Nature*, 598(7881), 411–414. <https://doi.org/10.1038/D41586-021-02818-7>
- Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G., Wiemann, M. C., & Chave, J. (2009). Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. <https://doi.org/10.5061/dryad.234>
- Zhou, Y., Bomfim, B., Bond, W. J., Boutton, T. W., Case, M. F., Coetsee, C., Davies, A. B., February, E. C., Gray, E. F., Silva, L. C. R., Wright, J. L., & Staver, A. C. (2023). Soil carbon in tropical savannas mostly derived from grasses. *Nature Geoscience*, 16(8), 710–716. <https://doi.org/10.1038/s41561-023-01232-0>
- Zhou, Y., Singh, J., Butnor, J. R., Coetsee, C., Boucher, P. B., Case, M. F., Hockridge, E. G., Davies, A. B., & Staver, A. C. (2022). Limited increases in savanna carbon stocks over decades of fire suppression. *Nature*, 603(7901), 445–449. <https://doi.org/10.1038/s41586-022-04438-1>

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